XI.—*Remarks on the Cœlenterate Nature of the Sponges.* By William Marshall*.

On different occasions I have given expression to my conviction that the Sponges are Cœlenterata—a conviction which I share with Leuckart, Häckel, Von Lendenfeld, and others. It originates from a series of morphological and ontogenetic facts, of which radial symmetry is not the least important. I have formulated my opinion about as follows:—that the Sponges are Cœlenterata, in which, in consequence of the (phylogenetically speaking) very early occurrence of sessility, profound retrogressions had taken place, induced especially by a colossal overgrowth of the mesoderm.

Quite recently treatises have appeared from two sources on the systematic position of the Sponges. One of them (which certainly completely ignores my conception and its results) argues against the Sponges belonging to the Cœlenterata, and indeed to the Metazoa at all; while the other arrives at the result that, if the Sponges and Cœlenterata did possess common ancestors, the former must have branched off from the latter at a time when true typical Cœlenterate characters had not yet been acquired. As both treatises have distinguished spongiologists for their authors they call for the greatest consideration; and this the more, because they diverge so widely from each other in the result of their deductions. One of these memoirs is the work of F. E. Schulze †, the other of W. J. Sollas ‡; and although the former appeared somewhat later than the second, we shall here discuss it first, as its treatment of the subject is more general.

Schulze subjects the two opposite opinions—according to one of which the Sponges are colonies of Protozoa (Choanoflagellata), and according to the other Cœlenterata—to a thorough criticism.

Following the lead of James Clark and Carter, Savile Kent especially, with whom Bütschli has also recently associated himself, had taken it upon himself, on the foundation of observations partly correct, but partly also quite erroneous, to demonstrate the Protozoan nature of the Sponges, in which he laid particular stress upon the nature of the flagellate cells and the processes of development. The flagellate cells, when

* Translated from an advance copy, communicated by Dr. G. J. Hinde, F.G.S., of the paper in the 'Jenaische Zeitschrift,' Band xviii. pp. 868–880.

† Sitzungsb. Berl. Akad. d. Wiss. 1885, pp. 179–191; translated in Ann. & Mag. Nat. Hist. ser. 5, vol. xv. pp. 365–377 (May 1885).

‡ Quart. Journ. Microsc. Sci. n. ser. vol. xxiv. pp. 603–621.

fully developed, have, like the Choanoflagellata, a peculiarly differentiated frill (collar), which surrounds the basal part of the flagellum like a funnel, and also pulsating vacuoles in the interior. According to Kent the ciliated cells of the free-swimming larvæ also show the same characters; but this unfortunately has been seen by no one but himself.

Schulze, indeed, admits that it would seem hardly natural to suppose that so peculiar a structure as the collar of the flagellate cells had originated spontaneously twice in different groups of animals; but that it is to be regarded as inherited by the more complex, and therefore probably more recently differentiated form, from the simpler and therefore probably older form; but upon the whole he finds that, even if we leave out of consideration a series of differences, which certainly exist between the Choanoflagellata and flagellate cells of Sponges, it would not be a justifiable conclusion to deduce from a similarity, however close, of unicellular Protozoa with certain cells of the *trilamellate* Sponges, that the latter pertained to the former. Moreover, in reality, in the blastula of the Sponges flagellate cells of this kind, furnished with collars, are always deficient, although their presence there might justly be expected, if they originated from the *Choano*flagellata. After taking the trouble to examine how Savile Kent could have come to the erroneous assumption of the presence of the collar in the ciliated cells of the sponge-larvæ, Schulze arrives at the conclusion that the Sponges are true Metazoa, for they have sexual reproduction, and in their larvæ two different cell-layers, an outer and an inner one, may be clearly distinguished.

Schulze then discusses the hypothesis of the Cœlenterate nature of the Sponges. To the radiate structure occurring occasionally in larvæ and also in adults he ascribes no great importance; the Ascones never formed radial diverticula of their central cavity, and if these were produced in Sycones as sacciform distensions of the body-wall, it must be borne in mind that the Sycones before they formed the radial tubes possessed ontogenetically the pure type of the Ascones, so that the latter must consequently be regarded as ancestors of the former. Hence it seems very probable that the most ancient sponge-forms possessed an *Olynthus*-like form without radial diverticula of the central cavity; and the developmental history of the Sponges, so far as we are yet acquainted with it, presents no sufficient ground to justify the assumption put forward by me of common ancestors of the Sponges and Cnidaria, with radially arranged mesenterial pouches, tentacles with urticating capsules and indifferent aquiferous pores. It may be true that the difference between the free-swimming larvæ of

the Sponges, on the one hand, and the Cnidaria, on the other, is, on the whole, not more important than that between the various Sponge-larvæ among themselves. But as the fundamental differences in the structure of the two groups only showed themselves after the metamorphosis, we are justified in the assumption that the divergence of the two lines did not begin before that phylogenetic developmental stage which represents the ciliated larva on the point of metamorphosis.

Sollas takes quite a different standpoint, as strikes one at once on reading the proposition that he places at the head of his argument, namely, that it is difficult to suppose that such complicated structures as the collared flagellate cells of the Sponges could so closely resemble the Choanoflagellata, and at the same time be of independent origin. He explains the metazoic character of the Sponges, using Lankester's term, as "homoplastic," and their Infusorian character as phylogenetic, *i. e.* he believes the latter to be inherited, the former newly acquired. He proceeds:—Only two characters of the Sponges are essentially of metazoic nature, namely, the presence of both kinds of sexual reproductive bodies and of a gastrula. As regards the former, we find also in plants two kinds of sexual products, and what plants and animals could have formed independently of each other Sponges and Cœlenterata might also have acquired independently. In opposition to the second character, the formation of the gastrula, it is to be remarked, in the first place, that the flagellate cells of the habit of the Choanoflagellata occur very early in the ontogeny of the Sponges, at least before the formation of this gastrula, as is clearly the case in the amphiblastula of *Sycon raphanus*. Secondly folding, and therefore the formation of a gastrula, is one of the most frequent of all processes in the different developmental processes of animals, and is probably easily explicable by a simple mechanical process. So much, at least, is certain, that foldings in numerous cases originate quite similarly and independently of inheritance, and may lead to the foundation of organs which may indeed be "homoplastic," but certainly not homologous. Further, we see that the formation of a gastrula in Sponges, as also in Cnidaria, may take place in two ways, namely, by invagination and by cleavage of the mesenchyma, and one or other of these two modes at least cannot be explained by inheritance. Once more asserting the early occurrence of the cells like Choanoflagellata in the sponge-larvæ, Sollas comes to the conclusion that the Sponges may have developed themselves independently as a special phylum from the Choanoflagellata, and he proposes to separate them from the Metazoa under the name of "Parazoa."

Moreover, the gastrula of these Parazoa differs sufficiently from that of the Metazoa in the fact that in it the hypoblast (endoderm) consists of cells provided with collars.

This is essentially the course of Sollas's argumentation. It will be seen from it that he lays the chief stress upon the presence of the cells furnished with collars in the sponge-larvæ, and according to him they occur particularly in the amphiblastula of *Sycon raphanus*. I do not know whether Sollas has himself observed these collars in this case; except Kent, as already mentioned, no mortal has yet seen them; and so competent a judge as Schulze says * :—"In my investigations of the swarm-larvæ of *Sycandra raphanus*, which can hardly differ essentially in the structure of its larvæ from *Sycandra compressa*, and of many other sponge-larvæ, I have endeavoured, always in vain, to discover anything like the collar at the free extremity of the cylindrical flagellate cells." And he then shows very plausibly in what manner Kent's mistake may have originated.

My observations, which appear to agree with those of most other investigators, have shown me that flagellate cells always make their appearance in the canal-system of the Sponges only when a current of water through the body of the animal is possible, *i. e.* after the appearance of a gastro-vascular system with a double communication outwards. The flagellate cells are nothing but specially differentiated endodermic cells, which originally have exactly the same appearance as all the rest. This differentiation is due to division of labour: while the flat endodermic cells chiefly effect the inception of nourishment, the flagellate cells, by means of their flagella, produce an energetic circulation of water through the body of the sponge, and, chiefly by means of their collar, effect respiration. As in an Infusorian, an egg-cell, &c., the clear respiratory plasma † collects as much as possible superficially, and turned towards the point of access of the oxygen, so also in the flagellate cells of the Sponges, both in those of the swimming-larvæ and in those of the flagellate chambers. But while in the former the surface is more than sufficient for the reception of a sufficient quantity of oxygen, in the flagellate cells the case is different. They are therefore compelled to enlarge their respiratory surface. But where can this be done? Only where the cells come into contact with the water containing the oxygen. The rest of the body is more or less wedged in

* *Loc. cit.* p. 182 (Ann. & Mag. Nat. Hist. *loc. cit.* p. 368).

† See A. Brass, 'Biologische Studien, Th. I. Organisation der Thierischen Zelle,' pp. 64 and 150.

and enclosed between other tissue-elements; it is therefore the upper extremity, in which the clear respiratory plasma has collected, that is compelled to free itself from obstructive surroundings; the cell therefore loses its purely prismatic form and acquires a process which is accessible to the water on all sides. But this alone does not suffice, even if it widens upwards; it is compelled to enlarge its surface still more, and this is effected by its quitting its simple cylindrical or conical form and becoming converted into a funnel. This does not imply, as previous observers have sometimes stated, that the flagellate cells could not take in nourishment, but, as we see from the other endodermic cells, for that purpose they need not acquire a collar. Thus in my view there exists a very essential difference between the functions of the collar in the flagellate cells of the Sponges and in the Choanoflagellata, of which latter Bütschli remarks*:—"There is unanimity among observers that the collar, at least in the Cryptomonadina, is an organ connected with the reception of food."

In this way I come to the conclusion that the Flagellata and the flagellate cells of the Sponges absolutely stand in no phylogenetic connexion, but that the two peculiarities, which agree so remarkably, are due rather to adaptations *sui generis*. The flagellate cells of the endoderm of the young sponge, probably even in one which has originated from an amphiblastula, are not at once to be identified with the flagellate cells of the larva; first of all the flagella disappear, and then (after the cell has become flattened as an endodermic cell, and then again extended with a fresh accumulation of the clear respiratory plasma at the free pole), so soon as the flow of water becomes possible, they again make their appearance together with the collar; in the sponge-larvæ in which the endoderm is formed by division of the cœnoblastema—and these are probably the majority—there can be no question at all of any such connexion.

While I am perfectly in agreement with Schulze in denying any relationship between the Sponges and Choanoflagellata, our views with regard to the degree of relationship between the Sponges and Cnidaria are, as already remarked, very divergent, and I will now endeavour to support and establish my opinion in opposition even to such serious objections as Schulze puts forward.

As we have already seen, Schulze, while placing the ontogenetic processes in Sponges in the first line, as justly required

* Bronn's 'Klassen und Ordnungen,' Neue Bearb. Bd. i. p. 885.

by modern ideas, finds no sufficient grounds, in what we at present know of these, for ascribing, as I have done, to the common ancestors of the Sponges and Cnidaria radially arranged mesenterial sacs, tentacles with urticating capsules, and indifferent aquiferous pores. In opposition to this I might indicate that I have not definitely assumed the existence of the tentacles and urticating capsules, but I say * :— "*It may be difficult to ascertain whether the Sponges are or are not retrogressive as regards these organs* (*i. e.* urticating organs) *and the tentacles*; but in the attempt to demonstrate the Cœlenterate nature of the Sponges this is not of preeminent importance;" and further, "In case the ancestors of the Sponges ever possessed tentacles and urticating organs it is not difficult to understand how these might have been lost;" and, finally, "*It is indeed not impossible that the Sponges branched off at a developmental stage of the Cœlenterate stem, at which tentacles and urticating organs had not yet been differentiated.*"

Hence there remain two points, namely the radiate structure and the canal-system, which chiefly determine me to see Cœlenterates in the Sponges; and it may perhaps not be superfluous to discuss these characters here in detail.

In the first place we have to attempt to answer the question, How did the radiate symmetry of the Cœlenterata originate? The literature that deals with this subject is not considerable. There exists, indeed, a whole series of books and memoirs in which one would expect *à priori* to find statements relating to it; but they refer to the radiate structure in general, and do not enter upon its origin. Properly speaking Leuckart † alone has spoken in various places in some detail upon this point, and we shall therefore on the whole adopt his guidance in what follows.

If we imagine a creature of spherical, discoidal, conical, or cylindrical form, swimming (but entirely in the water, not at its surface), this, supposing it to possess a body composed of perfectly homogeneous substance, will always find itself in equilibrium. If we imagine, further, that the substance of the body does not remain homogeneous, that, for example, a heavier part is differentiated, this will place itself either exactly centrally, *i. e.* axially, or it must form a uniformly developed mantle around the lighter part. Or the substance

* Zeitschr. für wiss. Zool. Bd. xxxvii. p. 244.

† In various places in his 'Jahresberichte,' and, further, in his tract 'Ueber die Morphol. &c. d. wirbell. Thiere,' p. 14, and especially in Bergmann and Leuckart, 'Anat. physiol. Uebers. d. Thierreichs,' pp. 392 *et seqq.*

may break up into any number of parts, and then these, if they are not to disturb the equilibrium, must always collect in such a manner that every plane drawn longitudinally through the creature may divide it into two halves of equal weight and of the same structure. If the divisional parts are all of equal size, the mass of cells, except when it is of a conical form, has no anterior or posterior, superior or inferior, part founded on structure (although perhaps on movement) (*Blastula*). It is otherwise, however, when the divisional parts are of different sizes and of different weights, and are not sufficiently numerous for one set of them to group themselves round the other as a continuous mantle; then the larger ones, in order to preserve the equilibrium, as also the smaller ones, will arrange themselves in a particular manner (*amphiblastula* of *Sycon*), and in this way special regions of the body will orientate themselves. That at the same time a cavity may be formed by separation in the interior of the regularly constructed cell-aggregate, and that this may become filled with water, is of no consequence if only the parts of the wall remain in equilibrium. Matters remain the same if this cavity breaks through outwards, or if a portion of the hollow sphere becomes invaginated; whether a swimming-gastrula forms a central cavity by invagination or by perforation, its mouth must be placed centrally and the parts of the wall must arrange themselves around it and the primary stomachal space, so that here also the equilibrium remains intact. So soon as special organs become differentiated in our animal, even without its acquiring a definite permanent position of the direction of movement necessitating the distinction of upper and lower, right and left, and whether these organs are such as aid in the taking of food (tentacles), or complications of the digestive cavity (mesenterial sacs, gastral canals), or sexual organs, &c. &c., the central place being already occupied by the primordial stomachal space, these must always place themselves peripherally, occur in plurality, and group themselves in such a manner that the animal does not lose its equilibrium. In this way the radiate structure of the primitive swimming Cœlenterata was brought about. There is, however, another point that must not be overlooked in these considerations. A radiate structure is not only of great service, indeed to a certain extent indispensable, to free-swimming creatures of spherical or cylindrical form &c., on account of the stability of equilibrium, but it may also be of great importance to sessile forms, inasmuch as, acting externally, it harmoniously increases the power of resistance in all directions; we construct not only our air-balloons on the radiate type, but also

our towers and other fortifications. In these considerations I have left the Echinodermata out of the question. They and the Cnidaria are only distantly related; the two classes have acquired the radiate structure independently of each other, and it shows essential differences in them. If I divide a typical Echinoderm (with the fundamental number five) by a polar plane into two equal halves, so that the plane on my side, as far as the central point, halves a radius, it will halve an interradius on the other side of the central point; but in typical Cœlenterata (with the fundamental number four) I shall under similar circumstances always halve similar parts.

There is no doubt that free, moving Cœlenterata are more ancient than attached ones, just as all sessile animals, which are only conceivable in water, are descended from swimming forms. The inducement to adhesion lies in the impulse more or less inherent in all animals to save themselves labour and bodily exertion as much as possible, and it could only be given when such a superfluity of food occurred that the animals needed to take absolutely no trouble in seeking it. When we see that the polyps, even when they are adherent, as so many have been for a long time, have retained the tentacles and the radiate structure, we must assume that these are of preeminent importance; and this I believe to be the case especially with the tentacles, which, together with the urticating organs, play so important a part in the obtaining of nourishment. The other radiality may rather be secondarily retained, perhaps in correlation with the tentacles (as frequently, *e. g.* in *Hydra*, the radiate structure finds expression only in those organs); at least it is precisely in adherent forms, *i. e.* in those without free locomotion, that it is interfered with more frequently than in others in favour of an incipient bilateral symmetry (Fungidæ, *Flabellum*, developmental stages of corals, Hydroida, &c.). In the origination of an incipient bilateral symmetry another incident probably cooperates, at least in part, namely regular currents of water; an adherent radiate animal when growing in a constant current of water must naturally develop especially *one* axis, that which lies in the direction of the constant current, for in this way alone it offers the greatest resistance with the smallest expenditure of force (growth-energy). A further consequence of sessility is the possibility of an increased development of the mesoderm, especially the formation of heavy skeletal masses.

As soon as a change of function took place with the gastro-vascular apparatus, as in the Sponges, as soon as the nourishment was taken up by it, the tentacles, if they had

already been differentiated at all, were lost in all cases, and the radiate structure in most cases, and finally the mesoderm increased in growth to such an extent that, under certain circumstances, the stomachal space and the buccal aperture disappeared. That the ancestors of the Sponges were not for very long, if at all, provided with tentacles, which, indeed, are only secondary, may be readily admitted, but *they were at least bilamellar, and at the same time, as we may conclude from the retrogressions which continually occur, radiate; they had a buccal aperture and a stomachal space, from which gastral canals ran radially to open freely outwards, breaking through the ectoderm; and such creatures, to my mind, are under any circumstances true Cœlenterata.*

When Schulze refers to the developmental processes in *Sycon*, and comes to the conclusion that it is probable that the oldest sponges possessed no radial diverticula of the gastral space, but, like *Olynthus*, had a simple saccular form, we might point out in opposition to this that in many cases ontogeny is no absolutely true reflection of phylogeny, and that, especially the older an animal form (as in this case the sponges undoubtedly are), the more may the phylogenetic recapitulation in the individual development be effaced. I might also say that every true *Olynthus*, like a simple gastrula, is, as an ovate, cylindrical, or conical body, radiate, for through its polar axis we may draw an infinity of longitudinal planes, every one of which will divide it into two exactly similar halves; this, however, I will not do, seeing that although it is incontrovertibly true, it would sound something like an evasion. But this much is certain—the radial canals and their arrangement are not the exclusive, and perhaps not even the oldest, criterion, of a radiate structure in the Cœlenterata.

If, however, we look somewhat more closely into the processes of development, as shown, for example, in the admirable pictorial representations that Schulze* has given us of the ontogenetic processes in *Sycon raphanus*, it will not be difficult to recognize a true radiate structure in certain stages. I shall lay less stress upon the free-swimming larva with its girdle-ring of granular cells (Taf. xviii. figs. 3–5), although even in it a radiate structure is already expressed; but let the reader examine especially fig. 12 on Taf. xix., which represents a young *Olynthus* as seen from above. We look down upon the flattened oval extremity of a hollow cylinder, which is perforated excentrically by a round aperture leading

* Zeitschr. f. wiss. Zool. Bd. xxxi. Taf. xviii. & xix.

into the gastral space, and "*at the periphery of the obliquely truncated oscular area there appear symmetrically arranged quadriradiates*" (*loc. cit.* p. 288), and, indeed, six in number; the three rays which lie in the same plane are so placed that the two continuous ones, which constitute a curved axis, embrace the margin of the disk peripherally, while the unpaired one passes perpendicular to them centripetally and radially into the disk itself, and thus this oscular area is divided up into six regularly radiately arranged parts (antimeres). But if we remember what were the causes of the radiate structure it becomes clear that it is a matter of perfect indifference what parts of the animal-body may first show it; like bilateral symmetry it may manifest itself in any parts which are not situated in the central axis, and in this case one is as important as another. If the gastræa-theory be true, if of all the systems of organs, so soon as a further division of the animal-body occurred, the digestive cavity first developed, it is by no means logical to assume that the radiate structure would also have affected *it* first of all; perhaps quite the contrary may have been the case, for the gastral cavity was, in the first place, the central and axially situated organ *par excellence*, and it is much more probable that the displacements and radiate arrangements of the parts in the interest of the maintenance of the equilibrium of a swimming animal will have first of all made their appearance in the parietal parts situated around the stomachal cavity. And what does the developmental history of the recent Cœlenterata teach us? That it is of no consequence at all whether the radial arrangement of the cœlenteric apparatus is brought about by centrifugal diverticula from the gastral space, or by partition-like centripetally growing processes from the wall.

In my opinion the characters of the gastro-vascular apparatus furnish a still stronger proof of the Cœlenterate nature of the Sponges than the radiate structure, which only occurs occasionally, although certainly more frequently than people seem inclined to believe. The radiate structure may become effaced in consequence of very long-continued sessility, just as well as parasitism can eliminate the bilateral symmetry of animals; and if sessility is capable of completely suppressing an organ so unmistakably important as a gastral cavity, it is not easy to see why the radiate structure, which is of far less importance to *adherent* animals, should be preserved under all circumstances, or even with special frequency. But the other Cœlenterate character, the ramification of the gastral cavity in the developed animal in the form of centrifugally running canals opening freely outwards, is retained in a true

sponge under all circumstances. How long these canals may be, whether they perforate the thin wall of an *Olynthus* as simple apertures, or in other forms traverse the thick body-wall as a system of profusely branched and frequently anastomosing passages, is quite irrelevant, and depends solely upon the degree of development of the mesoderm. It might perhaps still be objected that the canal-system of the Sponges is developed in such different ways that it certainly cannot always take its origin from the primitive gastral cavity, but at least as often be formed by gaps which make their appearance in the mesoderm, and growing on centripetally and centrifugally, perforate the gastral and dermal surfaces of the sponge-wall only in the second line. But we must not overlook one thing: how is the gastrula of the sponge formed? In perfectly analogous ways: some by invagination, and with this process the formation of the gastral canals from the stomach outwards may be compared; the others by the appearance first of all of a cavity in the cœnoblastema and its subsequent breaking through outwards; and this may be placed side by side with the origination of the canal-system from gaps occuring in the mesoderm. I believe that the former process, as well as the formation of the gastrula by invagination, is the older and more typical, and that the second must be accounted for by some phenomena of adaptation *sui generis*.

In conclusion, I must again assert that it seems to me, so far as the conditions are at present before us, that the arguments which have been urged against the Cœlenterate nature of the Sponges are far from counterbalancing those which are in favour of it.

XII.—*On some Points in the Morphology of the Echinoderms, and more especially of the Crinoids.* By P. Herbert Carpenter, D.Sc., F.R.S., Assistant Master at Eton College.

In a recent number of the 'Revue Scientifique'*, Professor Edmond Perrier has published a short and semipopular article, the title of which appears in the table of contents as "Les Encrines Vivantes, d'après les Explorations du *Challenger*." The author's treatment of his subject, however, is not altogether in accordance with the expectations to which such a title gives rise; for his article is headed simply "Les encrines vivantes," and of the six columns to which it

* Revue Scientifique, tome 35, No. 22, 30 Mai, 1885, pp. 690-693.